THE GENERA OF VERNONIEAE (COMPOSITAE) IN THE SOUTHEASTERN UNITED STATES[1]

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VERNONIEAE Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88:** 203. 1819.[2]

Perennial or annual herbs, [shrubs, rarely trees or vines]. Leaves alternate, rarely opposite or whorled, sessile or petiolate. Heads homogamous, 1- to many-flowered, sometimes syncephalous, the receptacles flat or subconvex, usually smooth or pitted, rarely hairy, bristly, or chaffy. Flowers usually perfect; phyllaries many, in several series, closely or loosely imbricate, or rarely few and not imbricate. Pappus in one or more series, usually setose, the bristles in some genera flattened or rarely reduced or lacking. Corollas tubular (subligulate in *Stokesia*), tube elongate, limb with 5 narrow lobes, rarely (3- or) 4-lobed and slightly bilabiate, deep purplish-red, white, or blue [rarely yellow to orange in some Old World species], frequently glandular. Anthers with or without auriculate basal appendages; pollen grains echinate to lophate. Style branches slender, acute or slightly obtuse, uniformly and shortly hirsute, the stigmatic papillae on the inner surface toward the base (see Solbrig, 1963, *fig.* 2*c*). Achenes variable, terete to subterete, 3- to 10- (to 20-)ribbed or 4- or 5-angled. TYPE GENUS: *Vernonia* Schreber, Gen. **2:** 541. 1791.

A tribe of about 70 genera and 1500 species grouped into two to eight

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I am grateful to Drs. Wood and Miller for their editorial assistance, and to my associates at the University of Georgia, Nancy C. Coile and Anna Baker, as well as to my past and present graduate students who have worked toward developing a better understanding of this fascinating tribe. This research was supported by the University of Georgia and by several research grants from the National Science Foundation.

The illustration of *Stokesia* was drawn by the late Dorothy H. Marsh from plants sent from Mississippi by Dr. R. B. Channell and grown by Dr. Wood for the Generic Flora.

[2]The tribes of Compositae have been treated previously by O. T. Solbrig (The tribes of Compositae in the Southeastern United States. Jour. Arnold Arb. **44:** 436–461. 1963). The reader should consult this work for additional information (e.g., familial and tribal descriptions, notes, and references) not included here.

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subtribes with two centers of diversity: south-central Brazil and south-central Africa. About 21 species in *Vernonia, Stokesia, Elephantopus,* and *Pseudo-elephantopus* occur in the southeastern United States. Nineteen species are indigenous, while *Vernonia cinerea* (L.) Less. and *Pseudo-elephantopus spicatus* (B. Juss. ex Aublet) C. F. Baker are pantropical weeds. *Centratherum punctatum* Cass. is occasionally grown as an ornamental in the Southeast but probably has not become naturalized.

Members of the tribe can be distinguished by their generally alternate leaves; homogamous heads with one to many, usually perfect flowers (florets); tubular corollas (subligulate in *Stokesia*) that are deep purplish-red to blue or rarely white; and semicylindrical, long, slender, acutely tipped style branches that bear the stigmatic surface on their flattened inner surfaces. This type of style is found in all genera of the tribe.

One of the less well known tribes taxonomically, the Vernonieae have been recognized as a unit since 1817 (Cassini). Lessing's organization of the group formed the basis for De Candolle's classification of the tribe. Bentham and Hooker provided the next major revision, which was essentially followed by Hoffmann. Both Bentham and Hoffmann recognized two subtribes: Vernoniinae (Euvernonieae), with separate heads and distinct involucres, and Lychnophorinae (Lychnophoreae), with few-flowered heads aggregated into secondary heads as glomerules. Bentham also noted that subtribe Vernoniinae consists principally of one large genus, *Vernonia,* with a number of smaller genera closely connected and clustered about it. Philipson expressed dissatisfaction with the subtribal arrangement of Bentham, noting that retaining subtribe Elephantopodinae Cass. (1817) (maintained by both Lessing and De Candolle) was preferable to placing *Elephantopus* in subtribe Lychnophorinae. Philipson argued also for the separation of subtribe Rolandrinae. Jones (1977) concluded that Bentham's two subtribes, which are based on the presence or absence of the secondary aggregation of heads, was artificial and far from satisfactory.

More recently, Robinson *et al.* published a revised classification of the subdivisions of the tribe Vernonieae, emphasizing the value of chemical, cytological, and structural data that had previously been unavailable. They agreed with Philipson's separation of the subtribes Elephantopodinae and Rolandrinae. However, in the opinion of Gerald Smith (pers. comm.), a student of *Piptocarpha,* their delimitation of subtribe Piptocarphinae is probably unwarranted. The separation of subtribe Centratheranae is also unnecessary (Kay Kirkman, pers. comm.). For the present, these latter subtribes are better included in the Vernoniinae.

I agree with Robinson *et al.* in the exclusion of the Liabeae from tribe Vernonieae (see Jansen & Stuessy). The tribe Liabeae is a distinct group that is related to the Vernonieae but with significant differences.

Although delimitation of taxa above the rank of species in the Vernonieae is often difficult, series, sections, genera, and subtribes can usually be circumscribed due to significant discontinuities. For the most part, these groupings appear to be biologically meaningful, even though difficult to characterize.

Among the tribes of the Compositae, the Vernonieae, with their largely tropical distribution, are one of the least known cytologically (Turner, 1977a). Jones (1979) reported that chromosome numbers are known for 16 of the 70 genera of the Vernonieae. Genera with $x = 10$ predominate (five genera); three have $x = 9$, and others $x = 7, 8, 11, 13, 15$, and 17.

The Vernonieae encompass an impressive array of form, habit, and geographic distribution. The tribe includes one of the largest woody composites, the polymorphic *Vernonia arborea* Buch.-Ham. of India, Indochina, Malaya, southern China, the Philippines, and Indonesia. It reaches a height of 36 m (see Koster). At the other extreme, in the repeatedly burned grasslands of Africa there are acaulescent perennial species of *Vernonia* that are only 3 to 4 cm tall. *Pacourina edulis* Aublet is an aquatic with edible leaves. Although most species in the tribe are herbaceous perennials, subshrubs, or shrubs, others may be annuals, lianas, or trees. There is considerable variation in vegetative morphology attending the extensive speciation and wide distribution of the tribe, and there are both convergent and divergent trends among species of various climatic regimes. In contrast, many of the reproductive characters have remained remarkably uniform.

A notable exception to the uniformity of reproductive characters is the pattern of pollen sculpture. As first noted by Wodehouse and recently studied by several workers (Kingham; Keeley & Jones; and Bolick), the surface patterns of pollen of the tribe are taxonomically useful. Relative to pollen of other Compositae, the multiplicity of surface configurations in the Vernonieae is unusual, being approached in variability only in the Lactuceae, and the various patterns often provide a powerful tool for resolving taxonomic problems (Keeley & Jones). Sculpturing varies from echinate to lophate. The wall structure as seen by transmission electron microscopy resembles the Anthemoid pattern and is considered to be a modification of it (Skvarla *et al.*).

A number of Vernonieae have been surveyed for chemical constituents (Harborne & Williams). Flavonoids appear to be useful in the arrangement and characterization of species, series, and sections. Among the more interesting constituents are the sesquiterpene lactones, which are taxonomically useful at the subgeneric and generic levels and which have provided evidence for relationship between Old and New World species of *Vernonia* (Turner, 1981).

Little work has been done on the comparative morphology and anatomy of the Vernonieae. Metcalfe and Chalk mentioned several anatomical features of the wood of *Lychnophora, Piptocarpha,* and *Vernonia,* and Carlquist found mostly uniseriate rays and relatively long vessel elements in six genera. Other workers have noted that trichomes, venation patterns, and epidermal features of cleared leaves of *Vernonia* can be useful in discovering relationships (Faust & Jones).

Muller noted that pollen of the Compositae has been verified in the Oligocene and may date back to the Eocene. However, he stated that pollen of the tribe Vernonieae has not yet been found as a fossil. The family is likely of Gondwanalandian origin, and the tribe may be as well (see Turner,

1977a). The Vernonieae are probably most closely related to tribes Mutisieae, Cynareae, and Liabeae (Wagenitz; Robinson *et al.*).

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Key to the Genera of Vernonieae in the Southeastern United States

A. Corollas of outer flowers subligulate. ..... 2. *Stokesia*.
A. Corollas all tubular.
  B. Heads free from one another, not syncephalous. ..... 1. *Vernonia*.
  B. Heads united into glomerules, syncephalous.
    C. Pappus of straight bristles; glomerules broad. ..... 3. *Elephantopus*.
    C. Pappus of bristles, at least two of which are spirally twisted or doubly bent; glomerules narrow. ..... 4. *Pseudo-elephantopus*.

1. **Vernonia** Schreber, Gen. **2:** 541. 1791, nom. cons.

Erect perennial (rarely annual) herbs [shrubs, trees, or lianas]. Leaves alternate [rarely whorled or opposite], pinnately veined, usually cauline or sometimes mostly basal, the margins generally entire but sometimes remotely crenulate [rarely lobed]. Heads relatively small [sometimes large and showy], with ca. 10 to 80 flowers cymosely or paniculately arranged [in scorpioid cymes, or heads solitary and terminal]. Involucres cylindrical to broadly hemispheric or campanulate, composed of loosely or closely imbricated phyllaries arranged in several series, the inner phyllaries progressively longer. Receptacles flat to subconvex, naked. Flowers perfect; pappus in 2 series [sometimes 1], the outer pappus short, of scales or bristles [sometimes absent], the inner pappus of capillary, terete or slightly flattened, purple to straw-colored, often setose bristles. Corolla tube regular, elongate, with 5 narrow lobes, deep reddish-purple, rarely white or pink [blue, yellow to orange], often resinous dotted. Anthers exserted, sagittate at the base; pollen grains echinolophate to lophate. Style branches elongate, semicylindrical, apices acute, hispidulous with stigmatic papillae near the base on the inner surface. Achenes ribbed, usually resinous dotted. (Including *Seneciodes* Post & Kuntze, nom. superfl.; *Eremosis* (DC.) Gleason; *Leiboldia* Schlect.; *Monosis* DC.; *Lepidaploa* Cass.; *Suprago* Gaertner; *Behen* Hill; *Critoniopsis* Schultz Bip.). Type species: *Vernonia noveboracensis* (L.) Willd. Sp. Pl. **3:**

1632. 1803 (*Serratula noveboracensis* L.), typ. cons.; see Int. Code Bot. Nomencl. 1978, p. 402. (Named for William Vernon, 1680's–1710's, an English botanist who collected plants with D. Krieg in Maryland in 1698 and who was a correspondent of H. Sloane, J. Petiver, and R. Uvedale, among others.) —IRONWEED.

A largely tropical genus of some 800 to 1000 species, with 15 in our area. Species of *Vernonia* are considered to fall into two subgenera, each with four sections: subgenus VERNONIA is confined to the New World, while subgenus ORBISVESTUS S. B. Jones occurs in Africa, Madagascar, and southeastern Asia (Jones, 1979, 1981). Subgenus ORBISVESTUS is dibasic with $x = 9, 10$. The base number for subgenus VERNONIA has generally been considered to be $x = 17$, but Turner (1981), as the result of his work on a group of primitive vernonias from Mexico and Central America, has recently proposed a base number of $x = 10$. The two subgenera differ in sesquiterpene lactones, but Turner's work has suggested that there may be a connecting link among these compounds. The corollas of a few species of subgenus ORBISVESTUS are yellow to orange, a coloration unknown in subgenus VERNONIA. Further distinctions, as well as connecting links, are apparent from the distribution of pollen types within *Vernonia* (Keeley & Jones).

All species of *Vernonia* native to the southeastern United States have a chromosome number of $n = 17$; the introduced *V. cinerea* (L.) Less. has $n = 9, 18$. On a worldwide basis, the most frequent reports are $n = 9, 10, 17, 18, 20, 34, 51, 68$ (Jones, 1979).

Species of *Vernonia* native to the southeastern United States are herbaceous perennials, with the exception of the pantropical *V. cinerea* (*Seneciodes cinerea* (L.) Kuntze), a weedy annual. Although best represented in the tropics, vernonias are found in a wide variety of habitats and climatic regimes ranging from subtropical cloud forests and other wet areas to xeric sites in deserts, seasonally dry grasslands and savannas, and the temperate regions of eastern North America. Many of the species have distinct habitat preferences. For example, in our area, *V. Lettermannii* Engelm. ex Gray grows only on chert rocks along rivers of the Ouachita drainage system; *V. Blodgettii* Small is found in low pinelands in South Florida; *V. angustifolia* Michaux occurs on high sandy pineland; and *V. flaccidifolia* Small is encountered only in upland deciduous woods. Several other species (e.g., *V. gigantea* (Walter) Trel. ex Branner & Cov.) seem to be less restricted ecologically. The most important reproductive isolating mechanism in our species appears to be habitat, and the settlement of eastern North America with the resulting disturbance of the vegetation seems to have increased the frequency of hybrids.

I have made artificial F_1 hybrids in all combinations among all of the species of eastern North America (Jones, 1976). The hybrids are highly fertile, although F_2 breakdown has been detected among some F_2 combinations. Vigorous hybrids were obtained when our species were crossed with closely related ones from the highlands of Mexico, but pollen fertility was low because of irregular chromosome pairing at meiosis. The introduced *Vernonia*

cinerea is self-compatible, but our native species are not. Self-incompatibility and an annual habit help to account for the weedy character of *V. cinerea*.

Pollinators from several orders of insects, primarily Lepidoptera and Hymenoptera, are attracted in relatively large numbers to the flowers of *Vernonia* in both tropical and temperate regions. A list of insects associated with *V. Baldwinii* Torrey in Kansas is given by Schwitzgebel and Wilbur. Rusts of the genus *Puccinia* parasitize *Vernonia* (see Urban).

One of the more useful taxonomic characters is external pollen morphology (Keeley & Jones). There are six basic pollen types, the distribution of which appears to be correlated with evolution within the genus. In general, pollen types have been found to correlate well with classification schemes based on other morphological characters in defining the subsections of *Vernonia*.

The usefulness of sesquiterpene lactones and flavonoids as aids in the classification of the genus has been demonstrated by Mabry and associates. Sesquiterpene lactones provide remarkable systematic markers at the subgeneric and sectional levels, while flavonoids show great promise at the ranks of species and series.

Selected taxa of *Vernonia* have been examined by a number of workers interested in anatomical or morphological characters, including trichomes (Hunter & Austin, Faust & Jones, and Wild), anatomy (Alencastro), micro- and megasporogensis (Tiagi & Taimni), and gross morphology (Schaffner, Gleason, and Wagner). Aside from trichome characters, little of taxonomic value has been found.

Economically, *Vernonia* is of little importance. Several of our species (e.g., *V. noveboracensis, V. angustifolia,* and *V. arkansana* DC.) are used as ornamentals, as are a few African species. Some North American species (notably *V. Baldwinii, V. gigantea,* and *V. missurica* Raf.) can be weedy. Farmers in Alabama have told me that *V. gigantea* is a problem in pastures, and McCarty and Scifres have investigated many aspects of *V. Baldwinii,* which is a serious weed in Nebraska. Their reports provide information on the life history of this plant and its response to herbicides.

That the bitter sesquiterpene lactones of *Vernonia* are deterrents to herbivores was first demonstrated by Burnett *et al.*, who showed that rabbits and white-tail deer avoid *V. gigantea* and *V. noveboracensis,* both of which contain the sesquiterpene lactone glaucolide-A, but will eat *V. flaccidifolia,* which lacks sesquiterpene lactones. Glaucolide-A was also shown to deter the feeding of some but not all lepidopteran larvae.

Many *Vernonia* species have had wide use in folk medicine for treating a variety of diseases. The presence of active substances in these plants was demonstrated with the isolation of the sesquiterpene lactone vernolepin from the African species *V. hymenolepis* (Kupchan *et al.*). Vernolepin shows activity, both *in vitro* and *in vivo,* against carcinomas (see Kupchan *et al.*) and as an inhibitor of plant growth (Sequeira *et al.*). *Vernonia anthelmintica* (L.) Willd., from India, has been used as an anthelmintic and also has possible value as an industrial oil-seed crop. The achenes contain vernolic acid, which has potential as a stabilizer in plastics (Higgins). Work in connection with

developing this species as a crop plant has been reported by Berry *et al.* and Massey.

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2. **Stokesia** L'Héritier, Sertum Anglicum, 27. 1788.

Erect, somewhat branched, herbaceous perennials to 5 dm tall, stems glabrate below, pubescent above. Leaves alternate, minutely punctate; the upper reduced, sessile, and clasping; the basal larger. Heads large, showy, many flowered (with both ligulate and discoid perfect flowers), solitary or 1–7 in a corymb on terminal leafy peduncles; involucres hemispheric and composed of numerous pectinate-spinulose to foliaceous phyllaries (bracts) imbricate in several series, the outer phyllaries larger; receptacles flat, naked, somewhat fleshy. Pappus of 4 or 5 narrow paleaceous awns, soon deciduous from the achene but remaining enclosed in the head until corollas fall. Corollas blue (to purplish or white), resinous dotted, 5-lobed, the outer flowers ligulate, inner flowers tubular. Anthers included, appendages ovate; pollen grains echinolophate. Style branches long and slender. Achenes light brown, plump, 4-angled. TYPE SPECIES: *S. cyanea* L'Hér., nomen superfluum including *Carthamus laevis* J. Hill = *S. laevis* (J. Hill) Greene. (Named for Jonathan Stokes, M.D., 1755–1831, contributor to William Withering's *Botanical Arrangement of British Plants* and author of *Botanical Materia Medica* and *Botanical Commentaries*.)—STOKES' ASTER, STOKESIA, BLUE STOKESIA.

A monotypic genus endemic to the Coastal Plain of the southeastern United States. The range of *Stokesia laevis*, $2n = 14$, extends from Louisiana east of the Mississippi, across southern Mississippi and Alabama, into western Florida, northeastward across Georgia, and into southeastern South Carolina (see map in Gunn & White). *Stokesia* is frequently encountered in southern Mississippi and Alabama but is uncommon elsewhere. Its distribution across Georgia seems to be correlated with that of pitcher plant (*Sarracenia*) bogs with an underlying impermeable hardpan that holds moisture for at least part of the year. Elsewhere, this attractive plant grows on seasonally wet, sandy-peaty soil, in pine savannas and flat woods, and in hillside seepage bogs and adjacent sandy-peaty roadsides.

Stokesia, consistently regarded as a distinct genus, has always been placed

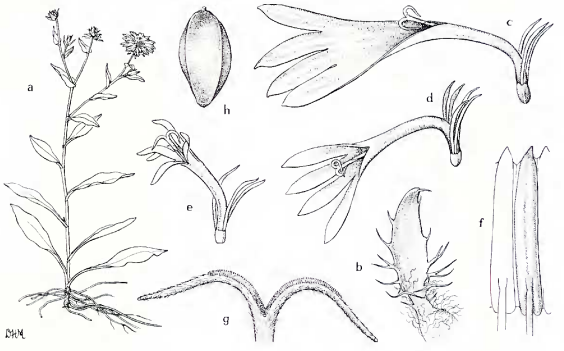

FIGURE 1. **Stokesia.** a–h, *S. laevis:* a, habit of flowering plant, × ⅛; b, involucral bract (phyllary), × 2; c–e, outer, central, and inner flowers, respectively, × 2; f, anther, abaxial side, × 10; g, style branches and stigmas, × 10; h, achene, × 10.

in the tribe Vernonieae on the basis of the features of its style branches and stamens even though the outer ligulate corollas (described by J. Small as "five-lobed palmate") differ from the usual tubular corollas of the Vernonieae.

Wodehouse presented the first illustrations of the pollen, noting a resemblance to the pollen of *Barnadesia* Mutis, of the tribe Mutisieae. However, the pollen is echinolophate with greatly reduced spines, a type commonly found elsewhere in the Vernonieae.

Stokesia has been reported (Mabry *et al.*) to contain the sesquiterpene lactone glaucolide-A, a compound also found in several North American species of *Vernonia*, thus further suggesting that, in spite of the ligulate outer flowers, *Stokesia* is properly included in the Vernonieae. However, the haploid chromosome number of $n = 7$ is unique in the tribe (Jones, 1979), and the chromosomes of *Stokesia* are much larger than those usually seen in the Vernonieae (Gunn & White; pers. obs.)

Stokesia is often grown as an ornamental perennial, especially in the eastern United States and in England. A number of color forms have been recognized. Cultivars include 'Blue Danube', 'Blue Moon', 'Caerulea', 'Lilacina', 'Purpurea', 'Rosea', 'Alba', and 'Silver Moon' (see *Hortus Third* and Gunn & White). In the southeastern United States the plants are semi-evergreen in winter, quite hardy, and easily maintained in the garden. Propagation is by either seeds or division.

The oil content of the achene of *Stokesia* is about 40 percent, and of this 70 percent is epoxyoleic acid (White & Gunn). Since epoxidized products

are useful as stabilizers for vinyl plastics, the U. S. Department of Agriculture examined the possibility of using *Stokesia laevis* as a source of oil and conducted the initial phase of crop development research. This work provided an estimate of seed yield and a discussion of agronomic advantages and disadvantages. However, neither the mode of pollination nor the breeding system is known, and both will have to be determined prior to any serious attempts at breeding agronomically useful cultivars.

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18–22. 1934. [Seven soap bubbles blown together produce a geometric pattern similar to the pollen of *Stokesia*.]

3. **Elephantopus** Linnaeus, Sp. Pl. **2:** 814. 1753; Gen. Pl. ed. 5. 355. 1754.

Erect perennial, simple or sparsely branched, pubescent-stemmed herbs from stout rootstocks. Leaves chiefly basal or cauline, the petioles usually indistinct, the blades elliptic to lanceolate or ovate, acute at the apex, attenuate at the base, margins entire to crenate or dentate. Inflorescences complex, composed of few-flowered heads arranged in bracteate glomerules; these, in turn, in terminal corymbose or somewhat paniculate groupings. Heads homogamous, with (1 or) 2–4 (or 5) perfect flowers; the involucre composed of 8 phyllaries in 4 decussate pairs; glomerules of heads subtended by bracts. Pappus composed of [scales or of 20–40 or] fewer than 15 straight bristles. Corollas blue or lavender to white, the tube slender, the limb unequally 5-cleft with a deeper fissure on the inner (adaxial) side. Anthers sagittate at base. Achenes ribbed or angled. (Including *Orthopappus* Gleason; excluding *Pseudo-elephantopus* Rohr. LECTOTYPE SPECIES: *E. scaber* L.; see C. F. Baker, Trans. Acad. Sci. St. Louis **12:** 44. 1902. (Name from Greek *elephas*, elephant, and *pous*, foot. Included by Linnaeus in a list of names expressing resemblance in his *Critica Botanica* [1739, p. 99] and in a list in *Philosophia Botanica* [1751, p. 179] headed "Habitus indicat similitudinem, qua excitatur idea, & ex idea nomen." Resemblance to an elephant's foot not otherwise explained.)—ELEPHANT'S FOOT, DEVIL'S GRANDMOTHER, TOBACCO WEED.

A genus of about 30 species centered in the Neotropics but also found in the Old World, with nine species occurring in North America and four of these in the southeastern United States (see Clonts & McDaniel; Jones in Cronquist). Although the genus is easily recognized, the species (which are based on characters of pappus, leaves, bracts, branching patterns, pubescence, and glomerules) are not always sharply defined and require some experience to identify. *Elephantopus carolinianus* Raeuschel and *E. elatus* Bertol. are restricted to the southeastern United States, while *E. nudatus* A. Gray reaches northern South America and *E. tomentosus* is distributed from Virginia to Texas and into Mexico. The single species of *Orthopappus*, *O. angustifolius* (DC.) Gleason, a plant of southern Mexico, the West Indies, and South America (south to Argentina and Chile), characterized by its numerous pappus bristles, is generally treated as a species of *Elephantopus*, but the two species segregated as *Pseudo-elephantopus (q.v.)* on the basis of their twisted or folded bristles are still being shuffled between the two genera.

The morphology of the inflorescence and the glomerules of *Elephantopus scaber* L. was described in some detail by Kunze. The main axis of the inflorescence or panicle is determinate. Each glomerule is terminal on its own stem and forms a part of a larger paniclelike inflorescence. Kunze noted that the branching pattern evident in the inflorescence is similar to that found within the glomerules, but the latter are very strongly reduced into a compact, complicated mass.

Kunze described the glomerule as a branch of the paniculate inflorescence so greatly reduced that each head appears to be sessile within its subtending bract; the whole thus forms a glomerule or "synflorescence." The bracts and florets are arranged in a tightly spiraling aggregate, making it virtually impossible to distinguish between the phyllaries and the subtending bracts. Kunze noted that many workers have been mistaken in thinking that the glomerule is subtended by three foliaceous bracts when, in fact, each bract subtends a panicle branch of its own. Thus, three greatly reduced panicle branches in close association form a glomerule. Overall, the inflorescence of *Elephantopus* seems to have been derived from a scorpioid inflorescence such as that found in many Neotropical vernonias.

Several sesquiterpene lactones (germacranolide dilactones)—for example, elephantin, elephantopin, elephantol, deoxyelephantopin, isodeoxyelephantopin, and molephantin—have been found in *Elephantopus*. Elephantopin has been shown to have significant activity *in vitro* against cells derived from human carcinoma of the nasopharynx, and *in vivo* against rat carcinomas (Lee *et al.*, 1981). It is believed that the sesquiterpene lactones that exhibit antitumor properties have general cytotoxic effects (Burnett *et al.*).

Chromosome numbers of $2n = 22$ and 44 have been reported for species of *Elephantopus*. The four species of *Elephantopus* occurring in the southeastern United States all have a diploid number of 22. James (1959) suggested that hybridization and introgression between *E. elatus* and either *E. tomentosus* or *E. nudatus* occur in Florida. The biology of the taxa is poorly known.

The genus has little economic importance, except for a few species that are weedy in some areas.

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4. **Pseudo-elephantopus** Rohr, Skr. Naturhist.-Selsk. Kjøbenhavn **2**(1): 214. 1792, "Pseudo-Elephantopus."[3]

Erect perennial herbs; stems solitary, branched. Leaves cauline, alternate, the lower larger, the others gradually reduced, pinnately veined, the petioles

[3]Although the spelling *Pseudelephantopus* has been widely used, the original spelling and hyphenation of the generic name must be retained. Article 73.9 of the *International Code of Botanical Nomenclature*, 1978, prescribes that "The use of a hyphen after a compounding form in an epithet is treated as an orthographic error to be corrected." In the paragraph of examples that follows, it is noted that "Art. 73.9 refers only to *epithets* (i.e., of species, of infraspecific taxa, or of subdivisions of a genus), not to *names* of genera or taxa of higher rank; a generic name published with a hyphen, e.g. *Pseudo-elephantopus* Rohr, can be changed only by conservation."

indistinct. Inflorescences terminal, bracteate, slender, racemose-spicate, with sessile glomerules of 1–5 heads on distal part of main stem and branches. Heads homogamous with 4 perfect flowers, the involucre of 4 pairs of decussate phyllaries (bracts), the 2 inner pairs almost equal, the 2 outer successively shorter. Pappus uniseriate, composed of 5–15 unequal or subequal bristles, some of the main ones doubly reverse-bent [or curled or loosely spiraled toward the tip]. Corollas bluish-purple to white, tubular-funnelform, the tube slender, the limb 5-cleft, deeply divided on one side, subligulate. Anthers sagittate at the base. Style branches slender, elongate, gradually pointed, minutely hispidulous, without conspicuous stigmatic lines. Achenes 10-ribbed. (Including *Distreptus* Cass., *Matamoria* La Llave & Lex., *Spirochaeta* Turcz., and *Chaetospira* S. F. Blake.) TYPE SPECIES: *Elephantopus spicatus* B. Juss. ex Aublet = *P. spicatus* (B. Juss. ex Aublet) C. F. Baker, Trans. Acad. Sci. St. Louis **12:** 45. 1902.[4] Name from Greek *pseudein,* false, and *Elephantopus,* elephant's foot.)—WHITE ELEPHANT'S FOOT, DOG'S TONGUE.

A neotropical genus of two closely related but quite distinct species, *Pseudo-elephantopus spiralis* (Less.) Cronq. and *P. spicatus,* $2n = 26$, the latter introduced into Florida some forty years ago.

Pseudo-elephantopus differs from *Elephantopus* in chromosome number ($2n = 26$ [$2n = 28$ also reported] *vs.* $2n = 22, 44$) and various morphological features (heads not held in a tight glomerule, subtending bracts leaflike, and pappus with at least two spirally twisted or doubly bent bristles *vs.* heads in tight glomerules with specialized subtending bracts and a pappus of straight bristles). Clonts, however, submerged *Pseudo-elephantopus* in *Elephantopus,* although others (e.g., Adams, Busey, Cronquist, Philipson, and Ward) have recognized it as distinct.

A number of authors have reported that *Pseudo-elephantopus spicatus* is a troublesome weed in tropical and subtropical areas. Fosberg first called attention to this species in Hillsborough County, Florida, and Blake warned that it is a potentially injurious weed that should be eliminated before it becomes thoroughly established. Ward, however, commented that "in no area of Florida has this plant yet given indication of the aggressive weedy nature manifested in other parts of its range." Widespread in the American tropics, *P. spicatus* is naturalized in Africa, eastern Asia, and Guam.

Little is recorded about the biology of the two species comprising this genus, but presumably the modified pappus bristles adhere to clothing and to the hair of animals, probably aiding in the spread of these plants. In Jamaica, the stalks and leaves of *Pseudo-elephantopus spicatus* have been used as brooms for sweeping houses.

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[4]Although Vahl (Skr. Naturhist.-Selsk. Kjøbenhavn **2**(1)**:** 216. 1792) gave a description of *P. spicatus* immediately after Rohr's generic description, he did not make the combination, because he referred to this plant as *Elephantopus.*

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